



Vegetation dynamics associated with changes in atmospheric nitrogen deposition and climate in hardwood forests of Shenandoah and Great Smoky Mountains National Parks, USA[☆]

T.C. McDonnell^{a,*}, S. Belyazid^b, T.J. Sullivan^a, M. Bell^c, C. Clark^d, T. Blett^c, T. Evans^e, W. Cass^f, A. Hyduke^f, H. Sverdrup^g

^a E&S Environmental Chemistry, Inc., PO Box 609, Corvallis, OR 97339, United States

^b Belyazid Consulting & Communication AB, Hyby Kyrkoväg 170, SE-233 76 Klågerup, Sweden

^c National Park Service-Air Resources Division, PO Box 25287, Denver, CO 80225-0287, United States

^d US EPA, Office of Research and Development, National Center for Environmental Assessment, Washington, DC 20460, United States

^e National Park Service - Great Smoky Mountains National Park, 107 Park Headquarters Rd, Gatlinburg, TN 37738, United States

^f Shenandoah National Park, 3655 US Highway 211 E, Luray, VA 22835-4702, United States

^g School of Engineering and Natural Sciences, University of Iceland, Sæmundargötu 2, 101 Reykjavík, Iceland

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ABSTRACT

Ecological effects of atmospheric nitrogen (N) and sulfur (S) deposition on two hardwood forest sites in the eastern United States were simulated in the context of a changing climate using the dynamic coupled biogeochemical/ecological model chain ForSAFE-Veg. The sites are a mixed oak forest in Shenandoah National Park, Virginia (Piney River) and a mixed oak-sugar maple forest in Great Smoky Mountains National Park, Tennessee (Cosby Creek). The sites have received relatively high levels of both S and N deposition and the climate has warmed over the past half century or longer. The model was used to evaluate the composition of the understory plant communities, the alignment between plant species niche preferences and ambient conditions, and estimate changes in relative species abundances as reflected by plant cover under various scenarios of future atmospheric N and S deposition and climate change. The main driver of ecological effects was soil solution N concentration. Results of this research suggested that future climate change might compromise the capacity for the forests to sustain habitat suitability. However, vegetation results should be considered preliminary until further model validation can be performed. With expected future climate change, preliminary estimates suggest that sustained future N deposition above 7.4 and 5.0 kg N/ha/yr is expected to decrease contemporary habitat suitability for indicator plant species located at Piney River and Cosby Creek, respectively.

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1. Introduction

Human activities have increased atmospheric emissions and deposition of nitrogen (N) and sulfur (S), altering ecosystems in the United States and elsewhere over the previous century (Galloway

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* Corresponding author.

E-mail addresses: todd.mcdonnell@esenvironmental.com (T.C. McDonnell), salim@belyazid.com (S. Belyazid), tim.sullivan@esenvironmental.com (T.J. Sullivan), michael_d_bell@nps.gov (M. Bell), Clark.Christopher@epa.gov (C. Clark), tamara_blett@nps.gov (T. Blett), Troy_Evans@nps.gov (T. Evans), Wendy_Cass@nps.gov (W. Cass), Abigail_Hyduke@nps.gov (A. Hyduke), hus@hi.is (H. Sverdrup).

and Cowling, 2002; U.S. EPA, 2009; Pinder et al., 2012). Aspects of climate, including air temperature and precipitation, are changing and influence the abiotic niches for plant and animal species. Global N and carbon (C) cycling have been substantially altered due largely to growth of human and livestock populations, production and application of N-based fertilizers, and combustion of fossil fuels (Schlesinger, 1997; Vitousek et al., 1997). Increased atmospheric N and S emissions, and subsequent deposition to terrestrial ecosystems, have altered competitive relationships among plants, decreased plant species richness and evenness, and adversely impacted some N-efficient species and favored some nitrophilous ones (Bobbink et al., 2010). Atmospheric emissions of C and N have also contributed to changes in climate, which are expected to

continue into the future (Intergovernmental Panel on Climate Change [IPCC], 2007; 2013, U.S. EPA, 2009). Changes in soil N availability, temperature, and precipitation influence plant species distributions (Parmesan, 2006), community composition, and biodiversity (Bobbink et al., 2010; Porter et al., 2013). Symptoms of nutrient enrichment have been documented in remote regions, including national parks and wilderness areas (Burns, 2003; Fenn et al., 2003; Geiser and Neitlich, 2007; McDonnell et al., 2014). These changes persist over time, and they can have long term consequences to the vegetation community composition.

Some plants react to atmospheric N deposition with increased growth and abundance, which can affect species diversity, threaten rare plants, and cause multiple ecological effects as other species are out-competed and eliminated from the plant community (Fenn et al., 2015). This is important to the National Park Service (NPS) because part of its mission is to maintain natural ecosystems unaffected by human influence for the enjoyment of current and future generations (Shaver et al., 1994). The response of terrestrial plant communities to change in N deposition can be influenced by climate (McDonnell et al., 2014).

The effects of acid and nutrient inputs combined with climate change on resources within national parks (NPs) have become important management concerns for the NPS (Porter et al., 2005, 2012), which is tasked with managing these public lands. Plant communities in eastern NPs have been subjected to decades of elevated S and N deposition. Two of these parks, Great Smoky Mountains NP (North Carolina and Tennessee) and Shenandoah NP (Virginia) have received among the highest levels of atmospheric S and N deposition of any national parks in the United States (Sullivan, 2017). In recent years, requirements of the Clean Air Act and other federal and state legislation and rules have resulted in air quality improvements in the region, including reductions in both S and N deposition (Sullivan, 2017).

The Clean Air Act provides special protection to maintain air quality related values in designated Class I areas, which receive the highest level of federal protection against air pollution damage to natural resources and include the Great Smoky Mountains and Shenandoah NPs. Native plant community composition represents one of the more sensitive air quality related values under the management of the NPS. Thus, it is useful for managers to know the levels of N deposition at which undesirable changes are likely to occur or persist under a changing climate.

A variety of dynamic modeling tools have been developed to assess impacts of climate and N deposition on vegetation composition (cf., de Vries et al., 2015). Among these, ForSAFE-Veg and VSD + PROPS (Smart et al., 2010; Reinds et al., 2014, 2015) are the two with the potential to be most generally applicable. Other analogous vegetation models have been developed for application to specific regions such as MOVE (The Netherlands; Latour and Reiling, 1993) and GBMOVE (United Kingdom; Smart et al., 2010). At the time of this study, the vegetation component (PROPS) of the VSD + PROPS model chain remained under development for applicability in the United States. As a result, the ForSAFE-Veg model chain was selected for use in this study with the intention of comparing ForSAFE-Veg and VSD + PROPS simulation results in future research. The ForSAFE-Veg model chain predicts future changes in plant communities and estimates the target load of atmospheric N deposition input required to reduce nutrient enrichment impacts and restore ecological integrity (Belyazid et al., 2011a, 2011b; McDonnell et al., 2014; Phelan et al., 2016; Rizzetto et al., 2016). Such modeling can inform discussions regarding N emissions controls within the context of a changing climate. ForSAFE-Veg dynamically simulates effects on vegetation community structure caused by changes in climate, atmospheric deposition of both N and S, and land management practices (Sverdrup et al.,

2007). Objectives of the research reported here were to:

- Develop a database of physiological traits and niche requirements relevant for plant species found at selected data-rich model sites in the two subject parks,
- Describe plant response and associated edaphic conditions related to biological effects caused by changing atmospheric deposition and climate, and
- Estimate target loads of N deposition required to avoid or mitigate ecosystem impacts beyond a specified threshold within a given time frame (year 2100). The definition for target loads used in this study is “the deposition load that is selected or determined to provide a level of protection for, or recovery of, sensitive ecosystem components based on a time frame for resource protection, feasibility of emissions reductions, and/or other considerations.” (CLAD Critical Load Definitions v1.1; http://nadp.sws.uiuc.edu/lib/CLAD/NADP_CLADdefinitions.pdf)

Model projections were used to evaluate interactions among changes in climate and nutrient input and to quantify the target load of N deposition that will protect park vegetation against further changes in biodiversity. The results of this study may be applicable to temperate forests throughout the eastern United States and elsewhere.

2. Methods

2.1. Sites

Model site locations and selected attributes are given in the [Supplementary Material, SM1](#). The Piney River site occurs within the Central Appalachian Montane Oak-Hickory Forest (Basic Type) vegetation association (Young et al., 2009; USNVC association code CEGLO08518). The habitat type at Cosby Creek is defined as Southern Appalachian Red Oak Cove Forest (USNVC association code CEGLO07878). The Cosby Creek site is at higher elevation (1217 m) and receives more average annual precipitation (1.7 m/yr) than the Piney River site (elevation = 895 m, precipitation = 1.4 m/yr).

2.2. Model overview

The model ForSAFE simulates the biogeochemical cycles of major forest soil elements (C, N, calcium, magnesium, potassium, sodium, chloride, aluminum) and also hydrogen and hydroxide ions (Wallman et al., 2005; Belyazid et al., 2011a). Although phosphorus (P) can be a limiting nutrient for plants, representation of P dynamics in ForSAFE was still under development during the time of this study and these sites lack sufficient data for including P dynamics. We also had no conclusive evidence that these sites were, or will become, fully N saturated. Therefore, the potential for P limitation was outside the scope of this study. The model is based on strict conservation of mass for all simulated elements. It solves mass balances by simultaneously and mechanistically estimating rates of biological processes, including photosynthesis, transpiration, growth, nutrient uptake, litterfall and decomposition. It also simulates abiotic processes including ion exchange, hydrology, mineralization, weathering and aqueous chemical reactions (Belyazid, 2006).

The model Veg simulates understory plant community composition and diversity in response to environmental conditions, physiological traits, and competition (Sverdrup et al., 2007; Belyazid et al., 2011a, 2011b). Interactions are based on estimates of species-specific rooting, shade casting and tolerance, and colonization characteristics as influenced by N supply and chemical and

climatic drivers. The plant community composition module Veg has been added to provide a linked model system with ForSAFE. The ForSAFE-Veg model chain can be used to assess the influence of external drivers on the composition and diversity of understory plant communities (Belyazid et al., 2011a; Sverdrup et al., 2012). The model chain has been recently applied in the United States (McDonnell et al., 2014; Phelan et al., 2016) and in Europe (Rizzetto et al., 2016; Zanchi et al., 2016) to simulate integrated responses of forest ecosystems to simultaneous changes in atmospheric deposition, climate, and forest management. The parameters in Veg are specified plant niches for light, moisture, temperature, N availability (i.e., soil solution N concentration), and pH, and physical/ecological traits in the form of rooting depth, shading height, and palatability. The Veg model determines how these niches and traits interact with simulated environmental conditions. The chemical (N availability and pH) and climatic (temperature, light below tree canopy, soil moisture) drivers are provided through ForSAFE, while the plant-specific niches specified in Veg are based on available empirical data and expert judgment.

2.3. Model parameterization

2.3.1. ForSAFE

2.3.1.1. Soils and forest growth. The upper 0.5 m of soil was modeled as the assumed main plant rooting depth (Sullivan et al., 2004). Soil texture for Piney River and Cosby Creek was derived from the Soil Survey Geographic (SSURGO) database (USDA-NRCS, 2015). Soil loss on ignition (an estimate of soil carbon), base saturation, and base cation weathering (determined with the MAGIC model; Cosby et al., 1985) were obtained from Lawrence et al. (2015). Soil physical characteristics including bulk density, mineral surface area, and water holding capacity were derived according to Balland et al. (2008). Values provided by Aber and Driscoll (1997) and Phelan et al. (2016) for northern hardwood ecosystems were used to parametrize canopy traits, photosynthesis, water balance, carbon allocation, biomass turnover, and tree tissue nutrient concentrations for modeling forest growth and associated nutrient uptake and litterfall.

2.3.1.2. Climate and deposition. Atmospheric deposition and climatic inputs to the model are given in Fig. 1. The most pronounced changes during the historical period (1850–2011) were for N and S deposition (Fig. 1a). Future changes in temperature were modeled to be substantial under some of the scenarios (described below). Forecasted changes in precipitation were more modest (Fig. 1b).

For climate scenarios, the PRISM database (<http://www.prism.oregonstate.edu/>) and the NASA Earth Exchange Downloaded Climate Projections database (NEX-DCP30; <https://cds.nccs.nasa.gov/nex/>) were used to develop time-series inputs of historical and future monthly air temperature and precipitation for the period between 1850 and 2100. From the NEX-DCP30 dataset, a future greenhouse gas concentration trajectory expected to result in an increase of 6.0 W/m² of radiative forcing by the year 2100 (RCP6.0) was selected from the Intergovernmental Panel on Climate Change, fifth assessment report (IPCC, 2013). The RCP6.0 scenario was used to represent anticipated future climate conditions based on an intermediate level of increase in radiative forcing. It is possible that these model sites will follow a different trajectory in future climate. Alternative climate inputs were specified as shown in the Supplementary Material, SM2.

All atmospheric deposition model inputs were determined as annual total (wet + dry) deposition. The baseline N deposition value for 1850 was assumed at a level of 1.0 kg N/ha/yr based on recent Clean Air Status and Trends Network (CASTNet) and National Atmospheric Deposition Program (NADP) measured values for

Alaska (<https://www.epa.gov/castnethttp://nadp.sws.uiuc.edu/>) and model baseline estimates by Holland et al. (1999). Baseline S deposition was based on the analyses of Husar et al. (1991; 3.0 kg S/ha/yr). The assumed 1850 level of S deposition was used to represent conditions shortly after the onset of the Industrial Revolution. Deposition of S prior to European settlement may have been lower.

Deposition sequences for N and S from 1850 to 1990 were developed based on scaling factors derived from emissions inventories using the Advanced Statistical Trajectory Regional Air Pollution (ASTRAP) model (Shannon, 1998) as applied by Sullivan et al. (2004, 2011), and Lawrence et al. (2015). The deposition sequences for Cosby Creek were based on ASTRAP data for the Coweeta Hydrologic Laboratory, North Carolina. Sequences for Piney River were based on ASTRAP applied to the Big Meadows deposition monitoring site in Shenandoah National Park. The N and S deposition estimates for the years 2002–2011 were taken from Total Deposition (TDEP) atmospheric deposition modeling (Schwede and Lear, 2014) as five-year averages centered on 2002 and 2011 to represent the overall trend in deposition during the period of available TDEP data (2000–2013). Deposition for individual years not derived from ASTRAP or Schwede and Lear (2014) estimates were obtained through linear interpolation. Additional detail regarding the historical deposition inputs for Piney River and Cosby Creek are available in Shannon (1998), Sullivan et al. (2004), and Lawrence et al. (2015).

Dry:wet ratios from Baker (1991) for the southern Blue Ridge Mountains were applied to interpolated NADP wet deposition of base cations and chloride (<http://nadp.sws.uiuc.edu/ntn/maps.aspx>) to derive estimates of total base cations (BC) and chloride (Cl) deposition at each modeling site. The BC and Cl deposition levels were assumed to be constant for all simulation years.

Future deposition was specified for the model scenarios based on assumed pre-industrial values, ambient conditions, and percent reductions from ambient conditions, generally following Tier III emissions reductions (U.S. EPA, 2014) implemented by 2025 and held constant thereafter to the year 2100. Alternate deposition inputs were specified for the scenarios as shown in Table 1. Four scenarios were modeled with ForSAFE-Veg, combining the deposition and climate scenario inputs as: Modern Climate-Pre-Industrial Deposition (MC-PID), Modern Climate-Modern Deposition (MC-MD), Modern Climate-Anticipated Deposition (MC-AD), and RCP6-Anticipated Deposition (RCP6-AD; see Table 2 for further definitions).

2.3.1.3. Additional nitrogen supply. N fixation was assumed to have contributed reactive N at both sites at a rate of 4.0 kg N/ha/yr, in general agreement with estimates of asymbiotic N fixation in this region (Cleveland et al., 1991, 2013; Galloway et al., 2004). The N fixation rate was assumed constant over time.

2.3.2. Veg

The version of Veg used here is based on the validated outcome of a previous application in the northeastern United States (Phelan et al., 2016), with a few modifications and development of a new metric to represent “niche alignment” (described below). All niches in the version used in this study are given as Gaussian distribution curves, described by optima and variability values; these can vary to allow for niches that do not follow a normal distribution (i.e., different tolerance levels away from the optimum). The niches are specified as:

$$Resp(driver, opt, var) = e^{-\frac{(driver-opt)^2}{var}} \quad (1)$$

where *Resp* (unitless) is the response of a given plant species to a

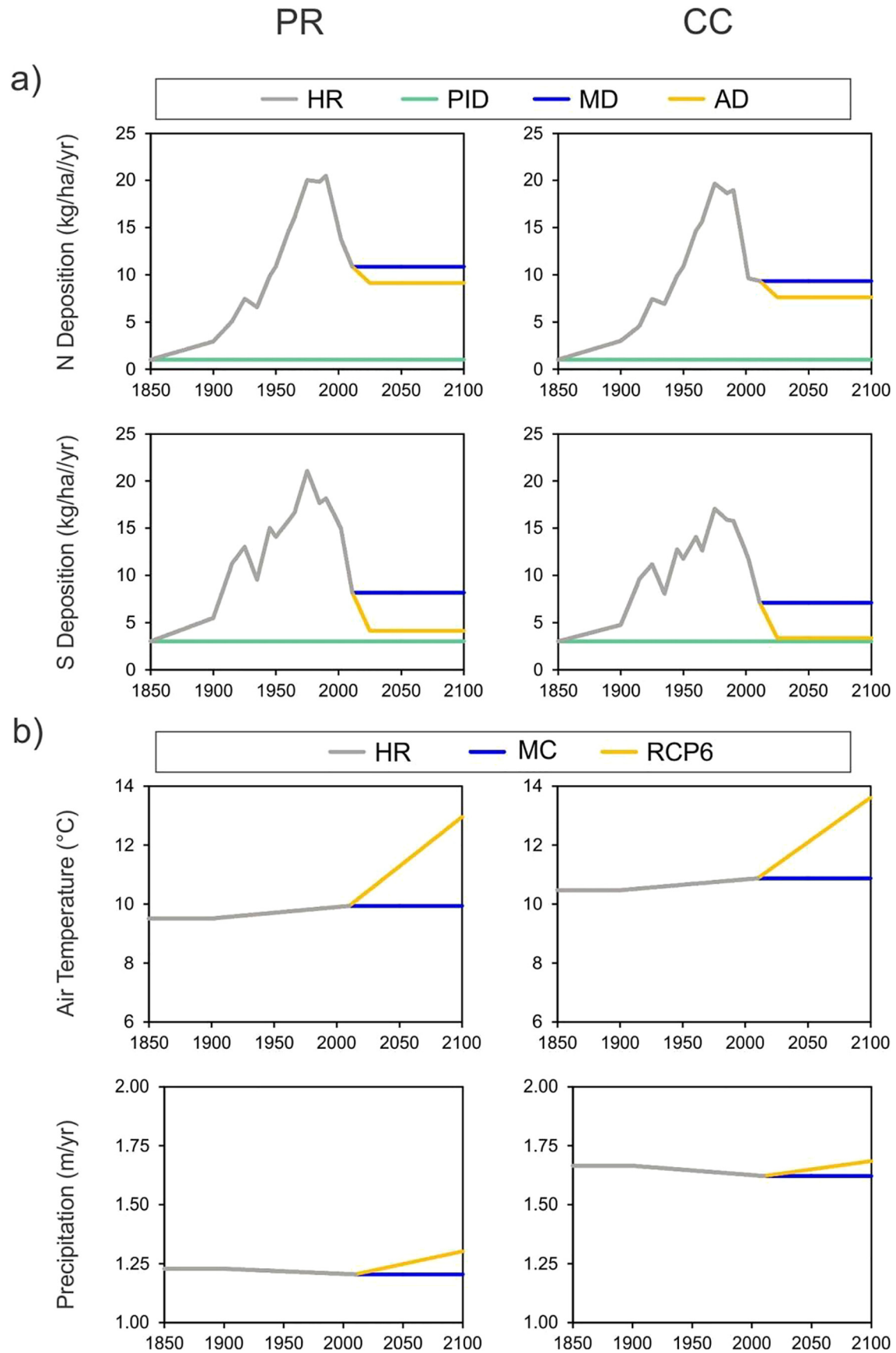


Fig. 1. ForSAFE-Veg model inputs for a) atmospheric deposition of nitrogen (N) and sulfur (S), and b) air temperature and precipitation. Results for Piney River (PR) are shown on the left, Cosby Creek (CC) on the right. See Table 2 for description of scenarios.

Table 1
Deposition scenario descriptions.

Scenario Name	Simulation Period	
	1850–2011	2011–2100
PID	Pre-industrial values (estimates for year 1850) held constant throughout the simulation.	
MD	ASTRAP historical reconstructions for select years between 1850 and 1990; TDEP 5-year averages centered on 2002 and 2011. All between years were linearly interpolated	TDEP 5-year average (2009–2013) constant.
AD	ASTRAP historical reconstructions for select years between 1850 and 1990; TDEP 5-year averages centered on 2002 and 2011. All between years were linearly interpolated	Linear ramp between 2011 and 2030 (defined by Tier III); then constant from 2030 to 2100

Table 2
Combined atmospheric deposition and climate scenarios used for ForSAFE-Veg modeling at Piney River and Cosby Creek, showing abbreviations used in the figures that present results.

Scenario ID	Climate Scenario ID	Deposition Scenario ID	Climate Scenario Name	Deposition Scenario Name
MC-PID	MC	PID	Modern climate	Pre-Industrial Deposition
MC-MD	MC	MD	Modern climate	Modern Deposition
MC-AD	MC	AD	Modern climate	Anticipated Deposition
RCP6-AD	RCP6	AD	RCP 6.0 Climate change	Anticipated Deposition

given *driver* (Five drivers: light, temperature, water, N availability, or soil pH), *opt* is the optimal value of the driver for the given species, and *var* (driver's unit²) is the variance of the plant response to the driver away from the optimum. The response (*Resp*) representing the extent to which the *driver* aligns with the specified niche for a plant can vary between 1 when the *driver* is equal to the optimum, and approach zero as the driver moves far from the optimum.

Vegetation surveys by Lawrence et al. (2015) were used to characterize understory plant communities (woody and herbaceous vascular plants <1.3 m height) at Piney River and Cosby Creek. Nine vegetation survey points were surveyed at each site on a 3 × 3 grid with 25 m spacing (Supplementary Material, SM3). At each of the nine points, three evenly spaced 1 × 1 m understory subplots were surveyed at a 1 m distance from the center point, totaling 27 understory vegetation sub-plots per site. Percent cover of understory plants was estimated using the Daubenmire (1959) cover scale for each species.

2.4. Indicators and response metrics

Vegetation response was modeled with Veg based on two sets of drivers: 1) climatic and edaphic factors that define niches relating to the five drivers: temperature, light, moisture, soil acidity, and N availability; and 2) physiological factors that affect plant competition and the morphology of the realized niches from four factors: colonization rate, rooting depth, shading height, and herbivore palatability. Physiological traits and niches for each modeled plant species were specified by on-site NPS botanists based on available data and expert judgement as described in the Supplementary Material, SM4. These two sets of drivers were combined and calibrated in the model to reproduce observations of relative abundance for all species that occur at each site. For Veg table calibration, the niche requirements provided by the experts were adjusted so that the simulated relative plant abundances were within 5% of the observations (See Supplementary Material, SM5, for details on Veg calibration and comparisons between simulated and observed soil chemical drivers). The abundance of each plant species, based on percent cover, relative to all other species present at the site (relative abundance) was derived by Veg using both sets of drivers (physiological traits and niche requirements).

For the purpose of this study, Veg produced a secondary metric of plant response, which we have termed the “niche alignment”. The niche alignment describes the suitability of a habitat to support

a given plant species. It represents the extent to which the five modeled abiotic drivers correspond with the known or suspected niche requirements for a given species, which is analogous to how the PROPS model (Wamelink et al., 2011; Reinds et al., 2014) uses five abiotic drivers related to soil acid-base chemistry, N availability, and climate to predict plant species occurrence probability. Niche alignment is dependent on the environmental and chemical drivers and does not consider the physiological traits of the plant other than the rooting depth. Soil solution pH, N, and soil moisture conditions are typically non-uniform throughout the soil profile and the plant specific rooting depths are used to determine access to these different conditions. Thus, rooting depth contributes to niche alignment via differences in the vertical distribution of N, acidity, and moisture. Niche alignment does not take into account interactions between a given plant and other plants that may be present at the site. It is therefore an indicator of the suitability of a habitat through the alignment of niches in response to environmental drivers, which are accessed by the plant-specific rooting depths in the case of the soil-based drivers (Fig. 2). The niche alignment is determined multiplicatively, rather than additively, among the individual drivers because if one driver is limiting (i.e., has a zero value) then the species cannot be expected to occur.

A group of indicator species was selected at each site ($n = 6$ at Cosby Creek; $n = 7$ at Piney River; Table 3) from among those considered characteristic of the respective vegetation association. Indicator species were selected from a set of characteristic species to represent a range of plant functional group types. Indicator species are defined here as a desired set of species indicative of the vegetation associations in which the model sites are contained. Details of the indicator species selection process can be found in the Supplementary Material, SM6. The three understory species with highest relative cover at Piney River (*Lindera benzoin*, *Rubus allegheniensis*, *Hamamelis virginiana*) were not available for selection as indicator species at that site because they did not meet sufficient occurrence criteria for building statistical response functions in a related research effort (McDonnell et al., 2018). Two of these three species (*Lindera benzoin* and *Hamamelis virginiana*) were not listed by Young et al. (2009) as characteristic species for the vegetation association in which the Piney River site is located. Niche alignment results for indicator species were combined into a single metric termed the habitat suitability index (HSI) for evaluating community response (Rowe et al., 2016). The HSI was determined as the average of the niche alignment values for the simulated set of indicator species. An increase in the value of HSI means that effective

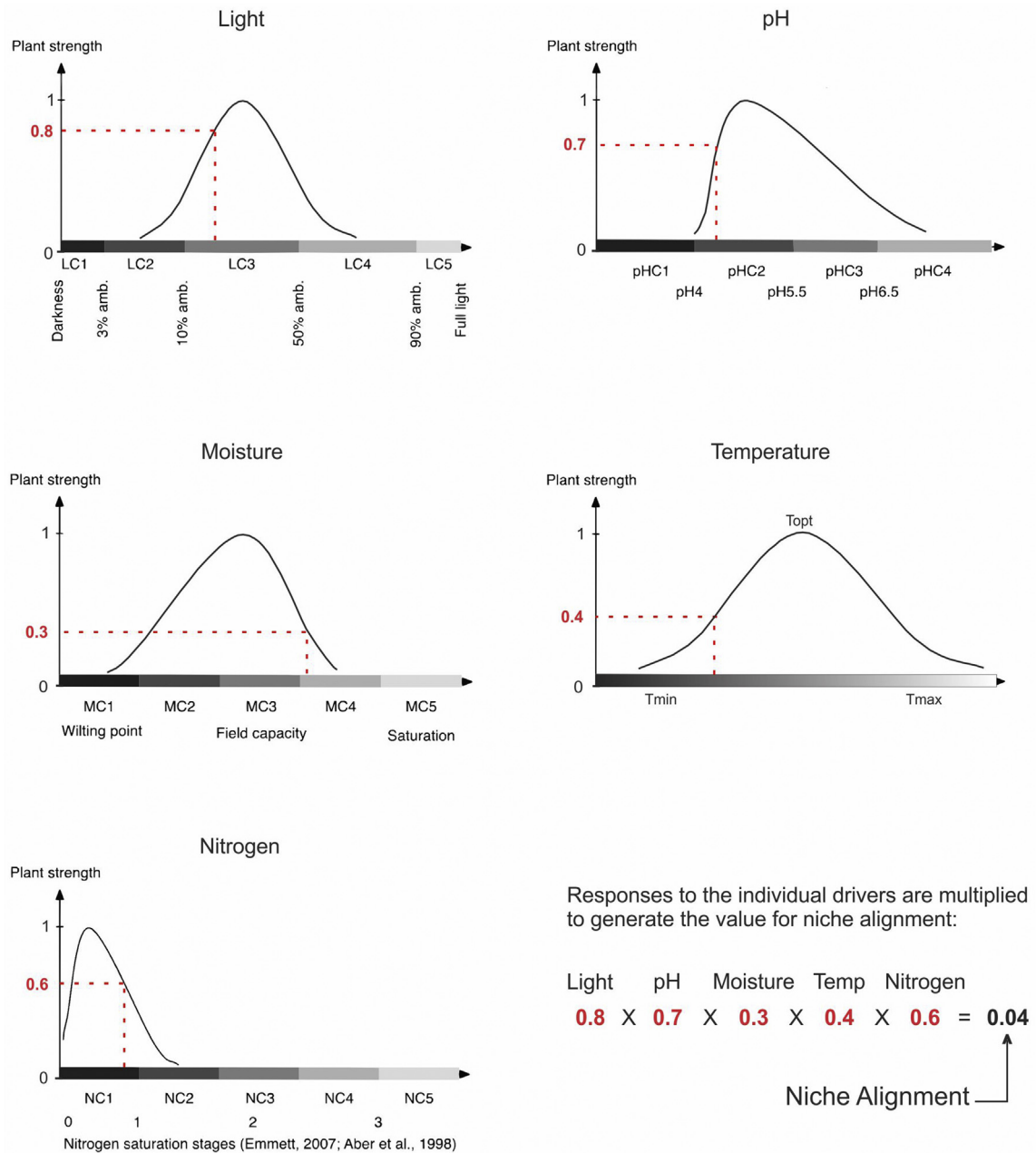


Fig. 2. Illustrative example of how niche alignment is determined with ForSAFE-Veg. Black lines indicate the specified niches for a hypothetical plant species. Red dotted lines and numbers indicate values for plant strength for a hypothetical model site/scenario. The rooting depth for each plant is used to determine the value expressed on the x-axis for pH, moisture, and nitrogen (Emmett, 2007; Aber et al., 1998).

abiotic conditions have become more favorable for the selected set of indicator species. The HSI assumes a value between 0 and 1, where HSI = 1 reflects environmental conditions that are optimal for all plant indicator species included.

2.5. Target loads

The ForSAFE-Veg model was used to establish preliminary estimates of the target loads of N deposition that are expected to protect an ecosystem from impacts beyond a specified indicator threshold within a designated time frame. Target loads were determined based on indicator species responses represented by the HSI. Target loads for the model applications at Piney River and

Cosby Creek were based on how N deposition in the range of 2–20 kg N/ha/yr is expected to impact the deviation between contemporary (year 2010) HSI and future (year 2100) HSI. The extent to which HSI is impacted under varying levels of N deposition was evaluated under two future climate scenarios: 1) no further change in the “Modern Climate” and 2) the anticipated climate change scenario adopted here (RCP6). This allowed for quantifying differences in target loads between a scenario of continued contemporary climate conditions versus expected future climate change. From these results, a target load can be selected to protect HSI against different amounts of change (e.g., no change in HSI, a 10% change in HSI, etc.).

Table 3
Selected indicator species for the habitat types at Piney River and Cosby Creek.

Model Site	Species Code	Scientific Name	Common Name	Life Form	Relative Cover (%)
Piney River	ACEPEN	<i>Acer pensylvanicum</i>	striped maple	Tree	2.5
	ACTRAC	<i>Actaea racemosa</i>	black baneberry	Herb	0.8
	CAROVA	<i>Carya ovata</i>	shagbark hickory	Tree	0.4
	FRAAME	<i>Fraxinus americana</i>	white ash	Tree	1.1
	HYDVIR	<i>Hydrophyllum virginianum</i>	eastern waterleaf	Herb	0.9
	PRUVIR	<i>Prunus virginiana</i>	choke cherry	Tree	1.7
	QUEALB	<i>Quercus alba</i>	white oak	Tree	0.3
	ACEPEN	<i>Acer pensylvanicum</i>	striped maple	Tree	4.2
Cosby Creek	ACESAC	<i>Acer saccharum</i>	sugar maple	Tree	6.5
	AGEALT	<i>Ageratina altissima</i>	white snakeroot	Herb	1.3
	LAPCAN	<i>Laportea canadensis</i>	wood nettle	Herb	19.1
	MAIRAC	<i>Maianthemum racemosum</i>	feathery false lily of the valley	Herb	2.3
	QUERUB	<i>Quercus rubra</i>	northern red oak	Tree	3.2

3. Results and discussion

3.1. Abiotic conditions

The niche alignment metric calculated by the Veg model is driven by air temperature inputs and four other abiotic drivers determined by ForSAFE: light availability, soil water saturation, soil pH, and soil solution nitrate (NO_3^-) concentration. We focus here on these abiotic results (Fig. 3). Note that although N and S deposition indirectly affect vegetation response by influencing soil chemistry, N deposition is not modeled as a direct abiotic driver of vegetation response. Rather, the soil solution N concentration is used, because that is what is experienced by the ground vegetation.

Simulated light availability to the understory plant community was between 30% and 50% for most of the simulation period at both sites. Effects of the simulated tree harvest in 1910 at Piney River are evident in the results for light availability and other modeled parameters. Soil water saturation was approximately 50% at Piney River and between 40% and 35% at Cosby Creek throughout the simulation period.

The most dramatic changes among the five abiotic Veg-model drivers were for soil pH and soil solution NO_3^- concentration, while light availability and soil moisture were relatively constant throughout the simulations (Fig. 3). Between 1900 and the late 20th century, soil pH decreased by more than 1.5 and 1.0 standard units at Piney River and Cosby Creek, respectively. Both sites showed projections of minimal pH recovery between about 1990 and 2040 due, at least in part, to continued elevated N and S deposition and progressive base cation depletion. Soil solution NO_3^- concentration followed similar trends at both sites, with substantial increases between 1950 and the late 1990s, followed by decreases between the late 1990s and the early 2000s. These patterns were mostly driven by changes in N deposition during this period. Future projections of soil solution NO_3^- concentration under all scenarios showed increases between 2010 and 2100, even though N deposition remained flat or decreased. Although the timing depends on the modeled scenario, both sites trend towards N saturation in the future with N deposition and mineralization outpacing biological N assimilation. Reductions in future N deposition decreased soil solution NO_3^- relative to continued modern deposition rates, but did not decrease solution NO_3^- to pre-industrial deposition levels. Soil solution NO_3^- concentrations in the year 2100 were projected to be highest in response to climate change at both sites, even with reductions in N deposition. This is because increased temperature and decomposition under a warming climate would release additional mineral N in excess of biological requirements (Melillo et al., 2017). Thus, simulated reductions in N deposition in the AD scenario were not sufficient to reduce NO_3^- leaching, relative to the

continued modern deposition scenario, when accompanied by climate warming. With or without future climate change, historical N deposition has contributed to an accumulation of N in the soil and biota. Consequently, forest nutrient cycling (uptake, litterfall, decomposition) increasingly fulfills biotic nutrient uptake requirements, allowing future deposition to move the sites further towards N saturation, which results in increased N leaching. Climate warming further exacerbates the ongoing N saturation response.

Measurements of soil solution chemistry were not available for model validation at these sites. However, both vegetation plots had measured soil pH (in DI water) and were located within small catchments for which nearby stream chemistry data were available for comparison. Given the differences between the simulated environmental matrix (soil solution) and the observed matrices (stream water and soil slurry), simulated and observed chemistry compared reasonably well (see Supplementary Material, SM5). To more fully address comparisons between simulated and observed chemistry, additional seasonal observations from the soil solution would be necessary. This shortcoming in the ability to confirm modeled soil solution chemistry contributes uncertainty to simulated biological response.

3.2. Biological response

3.2.1. Niche alignment and relative abundance

Five out of seven indicator species at Piney River were estimated to have zero or near zero niche alignment and relative abundance under the scenario that reflects continued N deposition at pre-industrial levels (PID; Fig. 4). White oak (*Quercus alba*) was simulated to have the highest niche alignment and relative abundance throughout nearly all of the PID scenario. Although niche alignment of white oak increased throughout the latter half of the simulation period, its relative abundance declined towards the end of the 21st century due to competition with other plants. For the other three scenarios at PR (MC-MD, MC-AD, RCP6-AD), simulation results were similar. Niche alignment for striped maple (*Acer pensylvanicum*) and white oak showed strong increases and decreases, respectively, in response to the clear cut logging in 1910, which reversed quickly as the canopy reclosed and soil solution N concentrations returned to pre-harvest levels. This is expected because striped maple is considered to be more tolerant of increases in light and N availability than white oak. These patterns were similar for the relative abundance of these two species. As N deposition levels, and associated soil solution N, began to increase after 1930, both striped maple and white oak declined in niche alignment and relative abundance because both species prefer lower N supply (N class of 1.5 and 2 for white oak and striped maple, respectively;

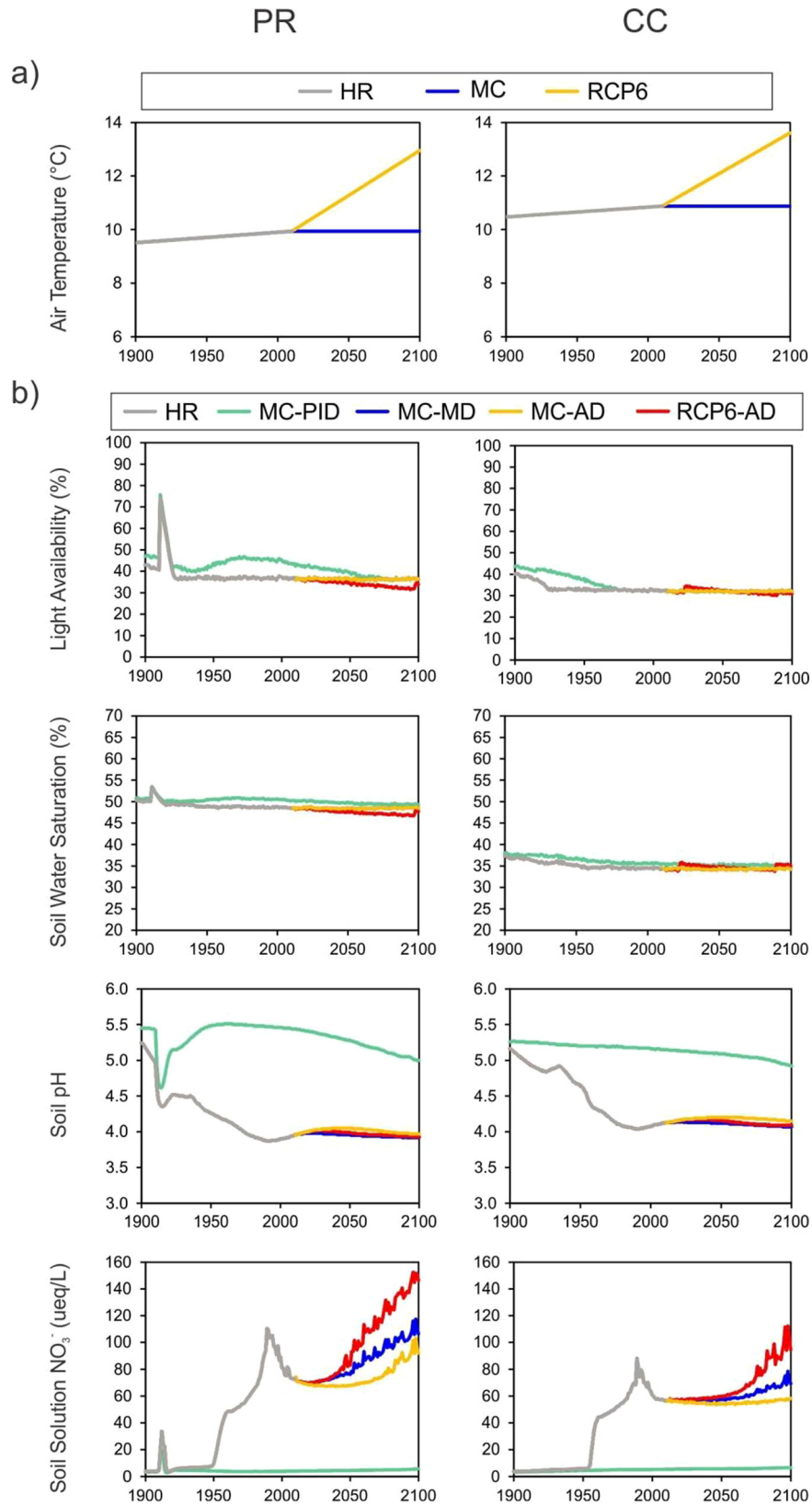


Fig. 3. Direct abiotic drivers used by the Veg model to determine vegetation response at the Piney River (PR) and Cosby Creek (CC) sites. HR is historical data records. See Table 2 for description of scenarios.

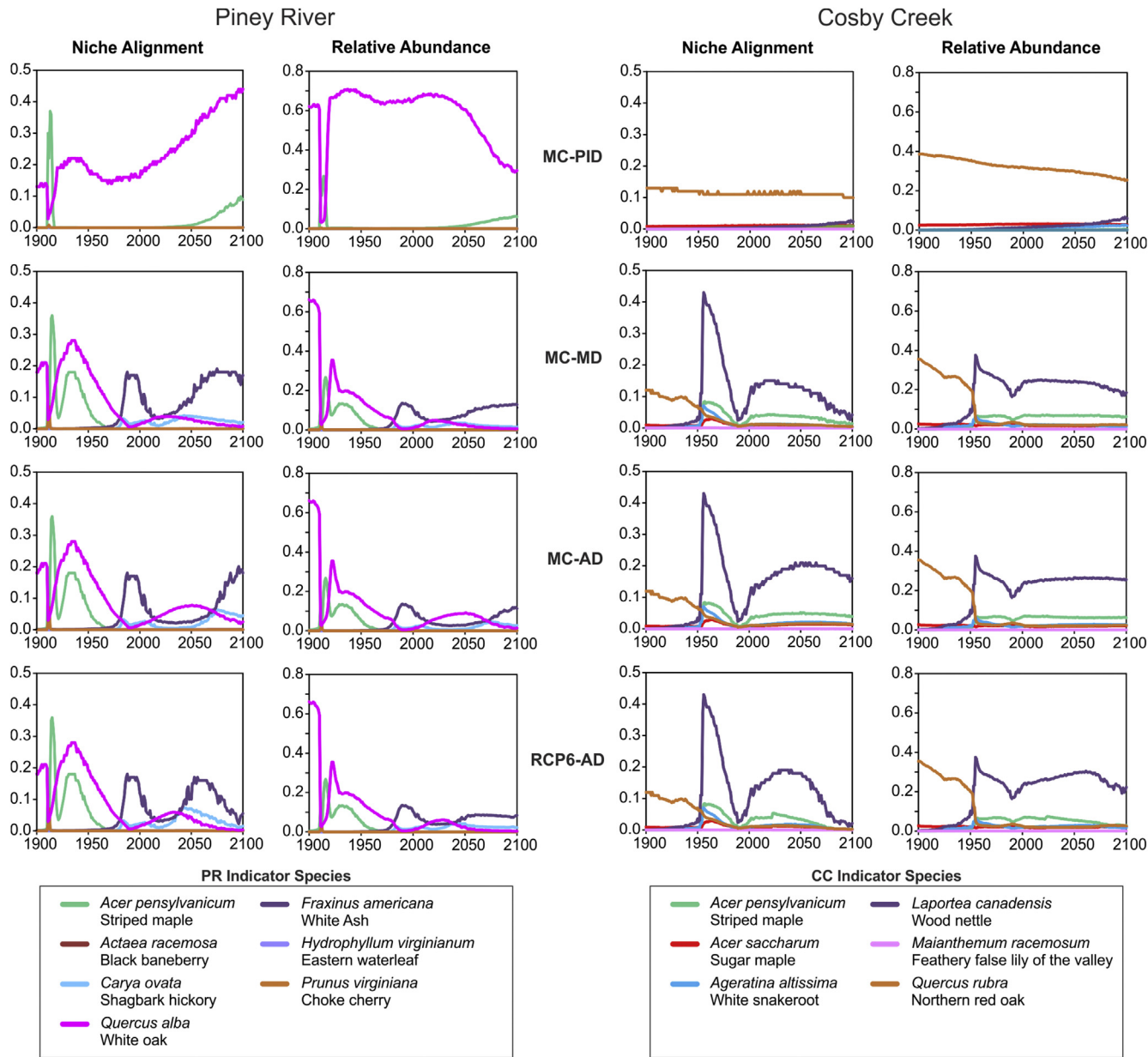


Fig. 4. ForSAFE-Veg model output for niche alignment and relative abundance of indicator species at Piney River (PR) and Cosby Creek (CC). Scenario labels for a given row of plots relate to all plots on the row.

Table SM3–1). White ash (*Fraxinus americana*), a relatively nitrophilous species, showed a sharp increase in niche alignment and, to a lesser extent, relative abundance from 1980 to 2000 when soil solution N increased under peak N deposition levels. These trends then reversed from 2000 to 2010 as soil solution N concentrations declined with decreasing N deposition. As the site moves toward N saturation, white ash was simulated to increase in the future to various extents depending on the modeled scenario. Although white ash is relatively nitrophilous, increases in soil solution N with increased mineralization caused by warming temperature (RCP6-AD) reached a sufficiently high level to cause a sustained decrease in niche alignment for white ash until the end of the simulation period. This end-of-century decrease was not reflected in the relative abundance for white ash because all species were negatively impacted by these high simulated soil solution N concentrations. The invasive emerald ash borer has been responsible

for widespread mortality of white ash canopy trees and saplings throughout the northeastern United States (Morin et al., 2017). Although, favorable future conditions for white ash seedlings may increase the potential for this species to reestablish in the forest canopy, canopy recruitment potential for orphaned cohorts of white ash seedlings is uncertain (Klooster et al., 2014). Similar results were observed under the scenario that reflected continued N deposition at pre-industrial levels at Cosby Creek. Only one species (northern red oak; *Quercus rubra*) showed niche alignment and relative abundance substantially greater than zero during the simulation period. The other three scenarios at Piney River and Cosby Creek (modern climate/modern deposition [MC-MD], modern climate/policy-driven deposition [MC-AD], and climate change/policy-driven deposition [RCP6-AD]) all showed similar responses between niche alignment and relative abundance. Niche alignment for northern red oak declined during the

early portion of the 1900s in response to deposition driven decreases in soil pH. Most of the species, particularly wood nettle (*Laportea canadensis*), were favored by the initial increase in N availability after 1950. However, as soil solution N concentrations increased, niche alignment for all species decreased to local minima prior to the end of the 20th century at the time of local maximum N availability. With ensuing decreases in soil solution N concentrations associated with reductions in N deposition at the turn of the century, sugar maple and wood nettle showed positive responses in niche alignment which persisted for the longest period of time with reductions in N deposition and no climate change (MC-AD). In general, the relative abundance results followed patterns that were similar to niche alignment. This suggested that including model representation of competitive interactions in addition to the abiotic drivers did not have a substantial impact on the interpretation of simulated vegetation response for these species and locations. Simulations involving alternate species and/or other environmental conditions may show larger differences between relative abundance and niche alignment.

3.2.2. Habitat suitability index

At Piney River, following the effects of the 1910 tree harvest, HSI showed a decreasing trend under the HR scenario during the mid-20th century, mostly in response to changes in niche alignment of striped maple and white oak. These decreases were mostly caused by increases in soil solution N and decreases in soil solution pH caused by elevated N and S deposition (Fig. 5). The latter part of the 20th century was characterized by increased HSI and increased soil solution NO_3^- concentration caused by elevated N deposition. This was driven mostly by the increase in niche alignment for white ash, as most other species were unaffected or negatively affected. There was a subsequent decrease in HSI between 2000 and 2010, largely in response to declines in N deposition. This suggests that the indicator plants at Piney River were at least temporarily promoted by the highest N deposition rates that occurred in the latter part of the 20th century. Future scenarios all showed initial increases in HSI between 2010 and 2100 (Fig. 5). The scenario of modern climate and decreased future N deposition (MC-AD) maintained a positive trend in HSI out to the year 2100. However, the relatively high soil solution NO_3^- concentrations under scenario RCP6-AD decreased HSI to below 2010 values by the year 2100, suggesting that expected future decreases in N deposition will not be sufficient to

maintain contemporary HSI at Piney River under a future climate driven by RCP 6.0. At Cosby Creek, HSI increased by more than five times at the onset of significant N leaching just after 1950 (Fig. 5). However, this increase was quickly reversed as soil solution NO_3^- further increased to peak concentrations around 1990. The simulated HSI recovered somewhat with decreased soil solution NO_3^- associated with recent deposition reductions. Future scenarios according to the MC-MD and RCP6-AD scenarios showed modest initial increases in HSI, then a consistent pattern of decreasing HSI to the year 2100 (Fig. 5). Anticipated reductions in N deposition maintained relatively high HSI by the year 2100 only if the climate does not change further (MC-AD). Even with anticipated reductions in N deposition, expected future climate change (RCP6-AD) was estimated to reduce HSI well below contemporary conditions, on par with the base case “do nothing further” emissions/climate scenario (MC-MD). This suggests that additional reductions in N deposition may be necessary to protect contemporary HSI against changes caused by climate. Additional climate mitigation (e.g., RCP 2.6 or RCP 4.5) would be expected to reduce the decrease in HSI simulated under the RCP 6.0 emissions scenario.

Simulation results suggested that anticipated climate and/or anticipated future N deposition will not be sufficient to counteract legacy effects of historical N accumulation and the trend toward N saturation at the model sites. In addition to future reductions in N deposition, active forest management such as thinning to remove tree biomass or soil carbon addition may help to reduce accumulated soil N and associated effects on understory vegetation. The feasibility of implementing such active management strategies is extremely limited due to the wilderness designation of these locations. Effects on future habitat suitability from additional reductions in N deposition are explored in the following section describing target loads.

The average niche alignment metric (expressed as HSI) results presented here are mainly driven by the response of only a few species that dominate the understory during each year. Confirmation of these species responses could be made with time-series measurements of the vegetation communities in the study areas. In the absence of such model confirmation, model results presented here should be considered preliminary.

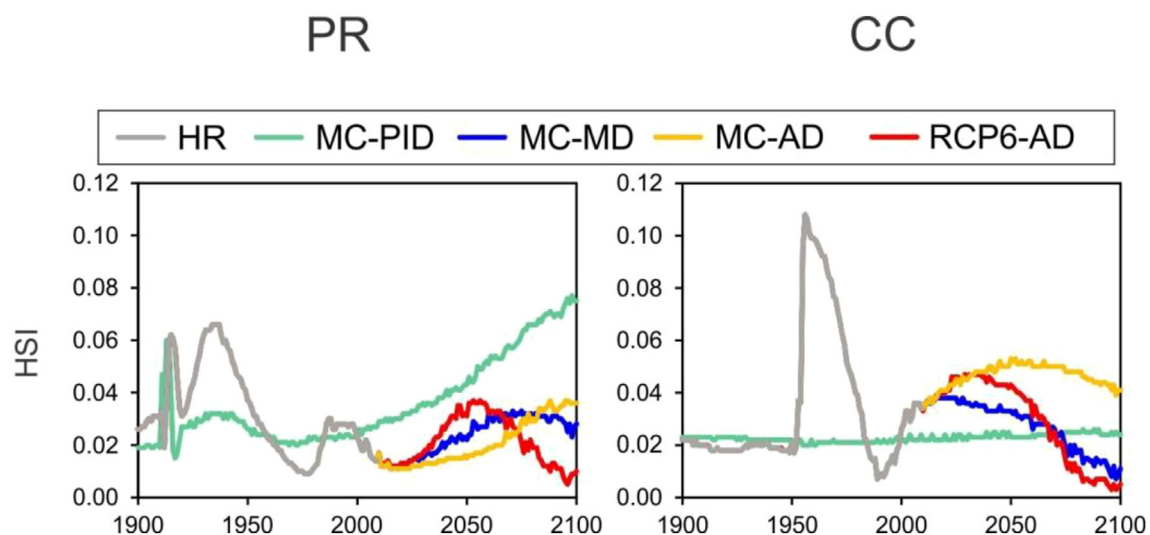


Fig. 5. ForSAFE-Veg model output for the Habitat Suitability Index (HSI) at Piney River (PR) and Cosby Creek (CC).

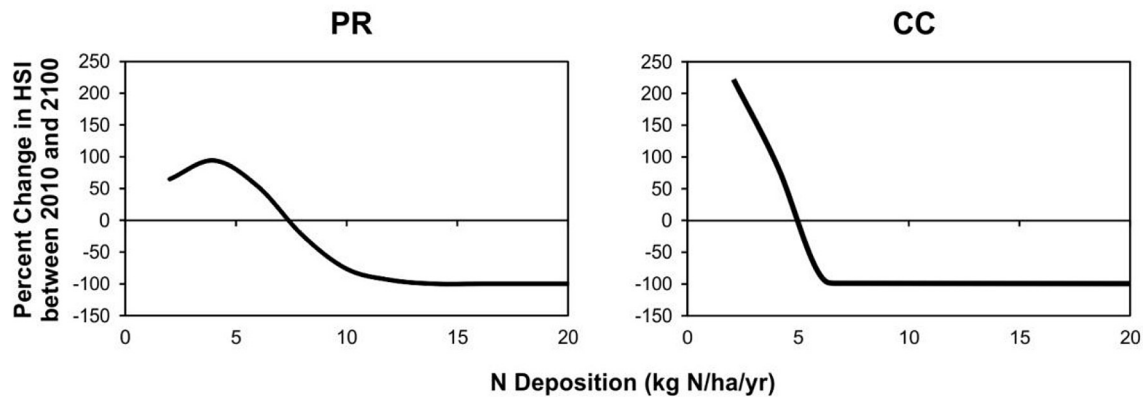


Fig. 6. Percent change in Habitat Suitability Index (HSI) between 2010 and 2100 under anticipated future climate change (RCP6) as a function of simulated future N deposition at Piney River (PR) and Cosby Creek (CC). Positive values indicate an increase in HSI between 2010 and 2100; negative values indicate a decrease.

3.3. Target loads

Under the scenario of expected future climate change, the model estimates of target loads to prevent year 2100 HSI from decreasing to below contemporary conditions were 7.4 and 5.0 kg N/ha/yr for Piney River and Cosby Creek, respectively (Fig. 6). Reductions in N deposition to levels below these preliminary target loads might be expected to increase future habitat suitability. Estimated target loads for protecting against a decrease in contemporary HSI were higher under the assumption of no changes in future climate (Supplementary Material, SM7). However, it is likely that future climate will continue to change. Further development of this case study might strengthen our ability to derive rigorous target loads using this modeling approach.

Future studies could develop target loads based on vegetation indices other than the HSI metric used in this study. For example, target loads could be determined from the response of all species that occur at a site or from the most sensitive species. Each of these choices will result in a different target load. Evaluation of the numerous possibilities for developing target loads was beyond the scope of this study.

4. Conclusions

Model results suggested that habitat suitability for the selected indicator plants at Piney River and Cosby Creek have undergone significant changes from 1900 to 2010. These historical changes in biological response appear to have been mostly driven by soil acidification and increased soil N availability associated with elevated N deposition. Existing rules and legislation designed to further decrease N deposition are expected to increase the HSI in the year 2100 relative to 2010. However, the future climate change scenario simulated here reverses this increase and results in lower year 2100 HSI relative to 2010 conditions. At least a portion of these future decreases in HSI caused by climate change could perhaps be offset by additional reductions in N emissions/deposition. There is a need to collect additional monitoring data that reflect changes in plant species assemblages over time, especially under changing levels of N deposition. Such data will be needed to confirm the veracity of model projections presented here.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.envpol.2018.01.112>.

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